

HABITAT USE BY THE BICKNELL'S THRUSH IN THE ESTRIE REGION, QUEBEC

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ABSTRACT.—Concern has been raised that the viability of Bicknell's Thrush (*Catharus bicknelli*) populations is precarious due, in part, to threats to its breeding habitat. Qualitative descriptions of habitat use have suggested that the species breeds primarily in dense, high elevation forests of northeastern North America. However, there is little quantitative information on habitat use patterns, which impedes formulation of effective conservation plans. To address this knowledge gap, we characterized the habitat of 42 sites occupied by Bicknell's Thrushes and 19 unoccupied sites on two mountains in the Estrie region, Quebec. Occupied sites were dominated by balsam fir (*Abies balsamea*) growing at high density, whereas unoccupied sites had a larger component of hardwoods at lower density. We found significant differences in vegetation composition and habitat structure between occupied and unoccupied sites for each mountain separately, and the two combined, though the particular variables distinguishing the two site types varied between the two mountains likely because of differences in management history. Our results show that the structure of occupied habitats may differ among sites even within a single region. However, it was evident that dense balsam fir-dominated habitats were used selectively by Bicknell's Thrushes at both study sites, and that the maintenance of such habitats should be a conservation priority in the Estrie region. Received 9 October 2001, accepted 6 June 2002.

Habitat loss and degradation is the most important threat to bird conservation (Bibby 1995). Among the approximately 10,000 extant avian species, 11% currently are susceptible of becoming extinct largely due to habitat destruction or deterioration (Collar and Andrew 1988, Doyle 1997, BirdLife International 2000, International Union for Conservation of Nature and Natural Resources [IUCN] 2000). Consequently, determining the habitat use patterns of species at risk is of crucial importance from a management perspective.

The Bicknell's Thrush (*Catharus bicknelli*) is one of the rarest birds in North America. Its breeding range is restricted to parts of southern Quebec, New Brunswick, and Nova Scotia in Canada, and New York and New England in the United States, and its population size has been estimated at 25,000–50,000

individuals (Rimmer et al. 2001). Due to limited numbers and its sensitivity to habitat degradation, the Bicknell's Thrush recently has been designated a species of special concern in Canada (Committee on the Status of Endangered Wildlife in Canada 1999, Dunn et al. 1999, Nixon 1999), as a top conservation priority in the northeastern United States (Rosenberg and Wells 2000), and as globally vulnerable using IUCN's criteria (BirdLife International 2000, IUCN 2000).

Our understanding of Bicknell's Thrush habitat use is based largely on qualitative information (but see Nixon et al. 2001). Within the United States, the Bicknell's Thrush is considered a strict habitat specialist, occurring almost exclusively in dense, high elevation forests dominated by small, stunted balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*; Wallace 1939, Atwood et al. 1996). In Canada, the species occurs in a wider variety of habitats, including some low elevation coastal and insular evergreen stands with a forest structure (i.e., dense conifers) similar to the higher elevation sites (Erskine 1992, Ouellet 1993). In recent years, the Bicknell's Thrush also has been observed in second growth forests, often with a significant component of hardwoods, following major logging or natural disturbance (Ouellet 1993, Nixon et al. 2001).

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Though the Bicknell's Thrush is of obvious concern to conservation biologists, there have been few quantitative studies of its habitat characteristics (but see Nixon et al. 2001), a necessary first step toward understanding the regulation of distribution and abundance. Our primary objective in this study was to provide a detailed, quantitative description of the vegetation composition and habitat structure of sites occupied and unoccupied by Bicknell's Thrushes on two mountains that represent strongholds for the species in southern Quebec, Mont Mégantic and Mont Gosford.

STUDY AREA AND METHODS

We conducted field work between 3 June and 16 July 1997, and 25 May and 28 July 1998 on Mont Mégantic (45° 27' N, 71° 09' W; 1,112 m maximum elevation) and Mont Gosford (45° 18' N, 70° 52' W; 1,189 m maximum elevation) which are part of the Appalachian Mountain range, near the Quebec-Maine border. Our study area at Mont Gosford included the Canadian portion of the Gosford massif, not just Mont Gosford itself. Marcotte and Grandtner (1974) provided a detailed description of vegetation types at Mont Mégantic, as did Pellerin (1986) for Mont Gosford. In general, high elevation areas on both mountains are dominated by balsam fir, with increasing abundance of hardwoods, including yellow birch (*Betula alleghaniensis*) and mountain maple (*Acer spicatum*), at lower elevations. Mont Mégantic has not been logged since the late 1950s, and the site now is a provincial conservation park (Marcotte and Grandtner 1974, Gouvernement du Québec 1988), while Mont Gosford was clear cut in some areas during the 1970s and thinned during the 1990s (Comité de Gestion Provisoire de la Forêt Habitée du Mont Gosford 1997).

Site selection.—We studied the elevational range of the Bicknell's Thrush along six routes: four on Mont Mégantic between 600–1,100 m elevation, and two on Mont Gosford between 700–1,090 m. These ranges closely correspond to the entire elevational ranges of both mountains.

We identified occupied and unoccupied sites first during point count censuses along the six routes between 9 June and 23 June 1997, and between 9 June and 2 July 1998. On 80% of census days, skies were clear and winds were weak at most; mist and light rain was intermittent on the other days. Point count stations were located at each 50-m elevation interval, or at most 200 m apart along the route. We surveyed each point count station for 8 min at least three times: twice during morning (04:30–07:30 EST) and once during evening (18:00–21:00), with 2–9 days between consecutive surveys. If we did not observe a Bicknell's Thrush at a station during the first three surveys, we conducted three additional surveys.

To increase our sample size, we identified additional occupied sites for habitat characterization during spot-

mapping censuses in five areas of 5–9.5 ha (mean = 7.3 ha), three on Mont Mégantic and two on Mont Gosford. Each area used for spot mapping was located where a Bicknell's Thrush was known to occur, and was censused 8–9 times, including 4–5 visits during morning and 3–4 visits during evening. Eleven of the 22 occupied sites at Mont Mégantic and 9 of the 20 occupied sites at Mont Gosford were located within the spot-mapping census areas, with 1–8 sites per spot-mapping area, and a minimum distance of 100 m between sites.

We considered a site occupied if we observed a Bicknell's Thrush on at least one occasion. Unoccupied sites were located either within the elevational range of the species where no Bicknell's Thrushes had been observed, or ≤ 100 m elevation below the lower limit of the elevational range. It was necessary to include sites below the lower limit of the elevational range in order to achieve sufficient sample size of unoccupied sites, but the distance was minimized to ensure that all sites were at relatively high elevation. We characterized a total of 22 occupied and 12 unoccupied sites at Mont Mégantic, and 20 occupied and seven unoccupied sites at Mont Gosford. The exact coordinates of all sites can be found in Connolly (2000).

Habitat characterization.—At each site, we characterized the habitat along a 50-m transect oriented at approximately 45° to the upslope-downslope axis. In occupied sites, the midpoint of each transect was located where a bird had been observed. In unoccupied sites, the midpoint corresponded to the position of the observer during the censuses. We recorded elevation for the midpoint of each transect using a Thommen altimeter (Thommen, Waldenburg, Switzerland).

We established 10 5-m $\times$ 1-m plots on alternating sides of each 50-m transect line, and chose five plots at random for detailed habitat characterization. In each plot we characterized eight vegetation composition variables and 22 habitat structure variables. For vegetation composition, the importance value of seven tree species and the shrub layer were calculated as the mean of the percentage of total basal area and the percentage of total number of stems accounted for by a given taxon within a 5-m $\times$ 1-m plot. We measured habitat structure variables to characterize the densities and cover of living trees, dead trees and fallen branches, tree stumps, herbaceous plants, mosses, ferns, lichens, bare rock, and leaf litter. We counted dead fallen branches across the entire 50-m transect. Detailed descriptions of each variable and how it was measured are provided in the Appendix.

Statistical analyses.—As a single estimate for each variable on a given transect, we used the mean value across the five plots. Our analyses aimed to fulfill two goals, (1) to provide a visual summary of how habitat structure and vegetation varied among occupied and unoccupied sites on the two mountains, and (2) to test whether the differences were statistically significant.

The first goal was achieved using ordination techniques. Detrended correspondence analysis (DCA) was designed specifically for vegetation data (Jongman et

al. 1995), and we used it for our vegetation analysis. DCA assumes unimodal distributions of plant species along gradients, and thus avoids the "horseshoe effect," which is an artifactual curvilinear relationship between ordination axes that often arises when other ordination techniques, such as principle components analysis (PCA), are used for vegetation data (Jongman et al. 1995). PCA is an ordination method ideal for variables that are expected to vary linearly along gradients (Jongman et al. 1995), and thus we used PCA to analyze the habitat structure data.

We performed the DCA of tree and shrub importance values (see Appendix) using Canoco ver. 4.0 (ter Braak and Smilauer 1998). Importance values were $\ln + 1$ transformed prior to analysis. We performed the PCA of the 22 habitat structure variables using SAS ver. 7.0 (SAS Institute, Inc. 1998). The variables CANOP, SCANOP, USHRUB, HERB, TOTC, DENS5, and DENS10 (see Appendix) were not transformed, LITTER was arcsin-square root transformed, and other variables were $\ln + 1$ transformed.

To test for differences between occupied and unoccupied sites (our second goal), we used discriminant function analyses (DFA). For the first two axes from each of the DCA and PCA (these represent the major axes of variation in vegetation and habitat structure, respectively), we performed DFAs for each mountain separately, and for the entire data set using SYSTAT ver. 6.0 (SPSS, Inc. 1996). The large number of variables relative to the number of samples precluded using the full set of variables in a DFA (Stevens 1996). The percentage of sites classified correctly by the discriminant functions was determined using both the entire data set, as well as with a jackknife technique in which sites were classified with functions calculated using all of the data except the site being classified (SPSS, Inc. 1996). Variables that contributed most to distinguishing between occupied and unoccupied sites were identified as those that were highly correlated with the discriminant functions (Stevens 1996).

RESULTS

We found Bicknell's Thrushes between 925 m and 1,100 m on Mont Mégantic, and between 775 m and 1,090 m on Mont Gosford. On Mont Mégantic, the percentage of sites occupied dropped markedly below about 925 m (96% above 950 m, 12% at 900–950 m, and 0% below 900 m). The pattern was more gradual on Mont Gosford (75% above 950 m, 67% at 900–950 m, and 56% below 900 m).

Significant differences between occupied and unoccupied sites were evident in the DCA of vegetation composition variables (Fig. 1), in the PCA of habitat structure variables (Fig. 2), and in the DFA (Table 1). In the DFA, the classification functions correctly identified $\geq 90\%$ of occupied sites and $\geq 79\%$ of unoc-

cupied sites using the raw data set (Table 1); the jackknife technique produced identical results.

Axis 1 of the DCA (Fig. 1) explained 39% of the variance in vegetation composition, and corresponded to a gradient from dominance by balsam fir at low values (occupied sites) to increasing importance of hardwoods at high values (unoccupied sites). While it appears that the importance of white birch (*Betula papyrifera*) was associated with occupied sites (Fig. 1), this result was due largely to only six sites (10% of all sites) which had either very large or small importance values, rather than to a consistent difference among occupied and unoccupied sites (see Connolly 2000). On Mont Mégantic, the difference in vegetation composition between occupied and unoccupied sites was greater than on Mont Gosford, as revealed both by visual inspection of the ordination diagram (Fig. 1) and by the stronger correlation of DCA1 with the discriminant function for Mont Mégantic (-0.93) relative to Mont Gosford (-0.67 ; Table 1). Axis 2 explained only 15% of the variance in vegetation composition, and did not appear to distinguish between occupied and unoccupied sites, or between mountains.

Patterns of variation in habitat structure among sites were relatively complex. PCA1, explaining 31% of the variation, corresponded largely to a gradient of tree density (DENS5, DENS10, TOTA, TOTB, TOTC), with low values on PCA1 indicative of sites with low density, tall canopy, and relatively abundant herbs and lichen (and vice versa, see Fig. 2). PCA2, explaining 20% of the variation, reflected a gradient from sites with relatively short shrub canopies, abundant snags (large standing dead trees) and moss, and relatively high tree density at high values, to the opposite conditions at low values. Both visual inspection of the ordination (Fig. 2), and the correlations of the PCA axes with the discriminant function (Table 1) showed that occupied and unoccupied sites were distinguished primarily along PCA1 on Mont Gosford, but primarily along PCA2 on Mont Mégantic (occupied sites at high values). As for Mont Mégantic, occupied sites at Mont Gosford tended toward higher values on PCA2 than unoccupied sites, though the difference was relatively slight.

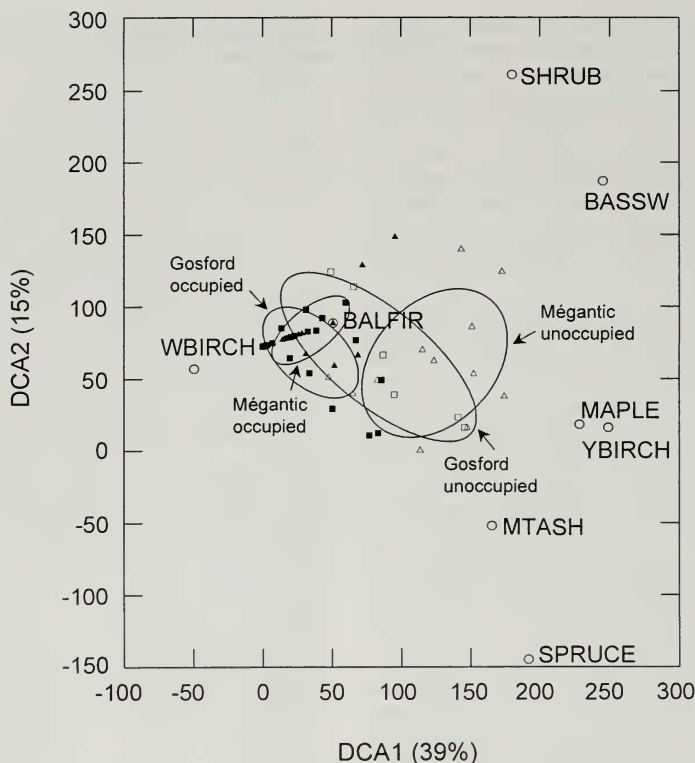


FIG. 1. Detrended correspondence analysis (DCA) showing variation in vegetation composition among sites either occupied ($n = 42$) or unoccupied ($n = 19$) by Bicknell's Thrushes on Mont Mégantic and Mont Gosford, southern Quebec, Canada. Axes 1 and 2 accounted for 39% and 15%, respectively, of the variation among sites. Ellipses represent Gaussian bivariate ellipses (± 0.7 SD) for each site type. Solid and empty triangles represent occupied and unoccupied sites, respectively, on Mont Mégantic. Solid and empty squares represent occupied and unoccupied sites, respectively, on Mont Gosford. Circles represent tree and shrub species.

DISCUSSION

Our study has provided one of the most detailed quantitative characterizations to date of the vegetation composition and habitat structure at sites both occupied and unoccupied by Bicknell's Thrushes in the same study area (see also Nixon et al. 2001).

Vegetation composition.—Bicknell's Thrushes selectively occupied high elevation coniferous stands; on Mont Mégantic and Mont Gosford we found Bicknell's Thrushes above 925 m and 775 m elevation, respectively, in forests dominated by balsam fir. Bicknell's Thrushes did not occupy stands with abundant hardwoods. In fact, mountain maple, yellow birch, and American basswood (*Tilia americana*) were entirely absent from occupied sites on the two mountains surveyed. Thus, the presence of these tree species may serve as a

crude indicator for the absence of Bicknell's Thrushes in forests of southern Quebec.

Recent surveys conducted in two other regions of Quebec, Charlevoix and Gaspésie, also indicate that Bicknell's Thrushes are unlikely to use mixed forest sites (Y. Aubry and GS unpubl. data). These results contrast markedly with Ouellet (1993), who reported observing more Bicknell's Thrushes in mixed than coniferous forests in Quebec. However, Ouellet (1993) did not provide quantitative criteria for distinguishing "coniferous" and "mixed" forests. In New Brunswick, Bicknell's Thrushes also were found in stands with a significant hardwood component, though at relative low densities (Nixon et al. 2001; D. Busby pers. comm.). Because pure coniferous stands in New Brunswick have been largely eliminated through logging, Bicknell's

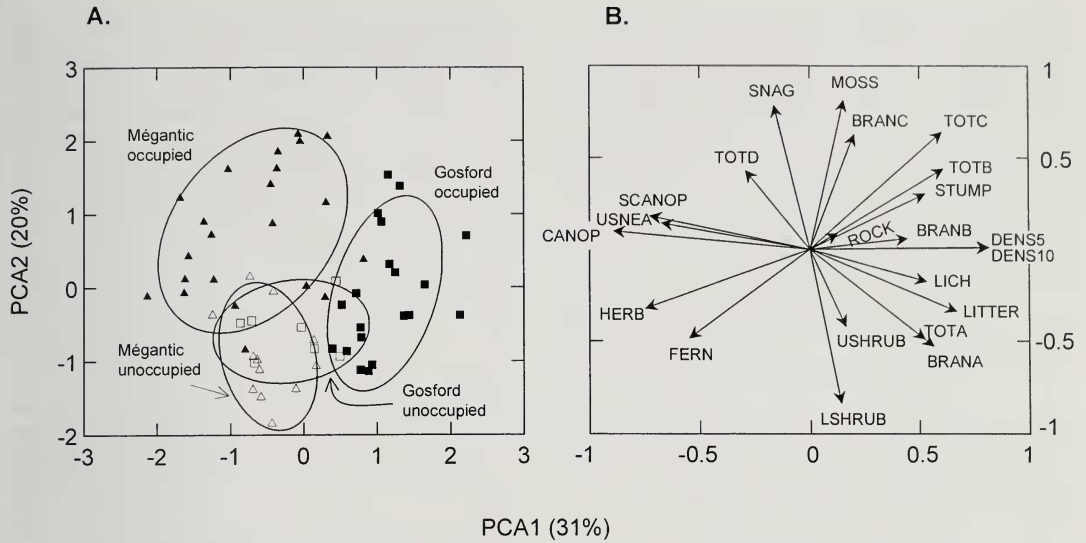


FIG. 2. Principal components analysis (PCA) showing variation in habitat structure among sites either occupied ($n = 42$) or unoccupied ($n = 19$) by Bicknell's Thrushes on Mont Mégantic and Mont Gosford, southern Quebec, Canada. Axes 1 and 2 accounted for 31% and 20%, respectively, of the variation among sites. Ellipses represent Gaussian bivariate ellipses (± 1 SD) for each site type. Solid and empty triangles represent occupied and unoccupied sites, respectively, on Mont Mégantic. Solid and empty squares represent occupied and unoccupied sites, respectively, on Mont Gosford. (A) Site distribution. (B) Factor pattern. The coordinate of the tip of a given arrow on a given axis is the Pearson correlation coefficient of the variable with that axis.

Thrushes might thus be constrained to use alternative habitat types. Together, these studies suggest that the Bicknell's Thrush uses dense

conifer-dominated habitats when available, but may use alternative habitats as well.

Habitat structure.—There were significant

TABLE 1. Results of discriminant function analyses (DFA) revealing significant differences between sites occupied and unoccupied by Bicknell's Thrushes on Mont Mégantic and Mont Gosford, southern Quebec, Canada, 1997–1998. Correlations are shown between each variable, ordination axes from a vegetation data analysis (DCA) and a habitat structure analysis (PCA), and the canonical function produced by the DFA.

Variable	Geographic comparison		
	All sites	Mégantic sites	Gosford sites
DCA1	−0.95	−0.93	−0.67
DCA2	0.29	0.42	0.06
PCA1	0.33	−0.16	0.94
PCA2	0.72	0.83	0.38
Wilk's lambda	0.42	0.22	0.36
Approximate F	19.05	26.38	9.57
P	<0.0001	<0.0001	0.0001
Eigenvalue	1.36	3.64	1.74
Group centroids			
Occupied sites	0.77	1.37	0.75
Unoccupied sites	−1.71	−2.51	−2.15
Correct classification - raw dataset (%; identical to jackknife results)			
Occupied sites	90	100	90
Unoccupied sites	79	92	86

differences in habitat structure between occupied and unoccupied sites in the Estrie region. Some of the measured variables that distinguished occupied from unoccupied sites may be directly related to habitat selection; others may be only correlated with the relevant habitat characteristics. Our data do not permit resolution of these alternatives, but they do allow interpretation of the potential relevance of different habitat characteristics in light of what is known about the species. The interpretations that follow focus on selected variables of potentially direct relevance to Bicknell's Thrush biology, and may be considered hypotheses that await further testing.

We have confirmed the use of habitat with very high tree density by the Bicknell's Thrush. Nest predation has been shown to be severe in certain areas and years (Wallace 1939, Rimmer et al. 2001), and the use of dense habitat might be beneficial in making visual detection by predators more difficult (Martin 1992). Sites occupied by Bicknell's Thrushes on Mont Mégantic also were characterized by a greater abundance of snags than unoccupied sites. Wallace (1939) noted large numbers of dead trees in habitat occupied by the species, and this may have been related to the severe climatic conditions prevailing at high elevations. Miller-Weeks and Smoronk (1993) found that most areas of high elevation spruce-fir habitat in New England and the Adirondack region of New York showed high levels of tree mortality during the 1980s. However, abundant snags may attract male Bicknell's Thrushes as they have been observed using snags as song perches (VC and GR pers. obs.).

Occupied sites on Mont Mégantic were characterized by greater percent ground cover of moss than unoccupied sites. This is typical of the wet and cool climate of high elevations (Reiners and Lang 1979, Sabo and Holmes 1983), and the correlation with Bicknell's Thrush habitat use may be related to nest construction. Wallace (1939) noted that the use of fresh moss was an outstanding structural feature of Bicknell's Thrush nests and that no other birds in that region (Mt. Mansfield) built nests with as much moss (see also Rimmer et al. 2001).

Differences between mountains.—We found striking differences in habitat structure, and to

a lesser degree vegetation composition, between occupied sites on the two mountains (Figs. 1 and 2). Contrasting histories of forest harvesting and management may be responsible for these differences. Because of more recent logging, forests on Mont Gosford are younger than those on Mont Mégantic, and therefore had a lower canopy, higher density, fewer snags, and less *Usnea*, a slow growing lichen (Fig. 2). Younger forests also typically are more diverse, consistent with our observation of a greater presence of spruce and white birch on Mont Gosford (Fig. 1). Recent logging may well be responsible for the greater similarity of occupied and unoccupied sites in vegetation composition at Mont Gosford than at Mont Mégantic. The differences we observed between mountains imply that the Bicknell's Thrush uses a range of vegetation composition and habitat structure conditions within dense balsam fir dominated forests.

Management and conservation implications.—The Bicknell's Thrush is a species of great conservation concern both locally and globally. Its future depends upon the conservation of both its breeding and wintering habitat. Our results provide new information relevant in this context.

We found that habitat used on different mountains, separated by only 30 km, can differ in vegetation composition and habitat structure. Thus, caution must be taken when assessing habitat suitability of a site on the basis of information obtained from another site or another region.

While our results show that the Bicknell's Thrush occupies mature as well as relatively young (25–40 year-old) second growth stands, it seems to prefer a specific vegetation composition within these forests, specifically a dominance of balsam fir and low density of several deciduous species. Silvicultural practices that would alter such vegetation composition are likely to be detrimental to the species. For example, recolonization of a logged site by balsam fir can be delayed considerably by the aggressive growth of species such as mountain maple (Archambault et al. 1998), thereby extending the period of time in which the habitat is unsuitable for Bicknell's Thrushes.

Though the Bicknell's Thrush shows some flexibility with respect to the structure of oc-

cupied habitat, it is consistently associated with high tree density. Precommercial thinning is a common silvicultural practice in coniferous forests, and consists of reducing stem density in young second growth stands in order to favor growth of the largest individuals of target species. Thinning likely has a negative impact on the Bicknell's Thrush by reducing the extent of very dense habitat. Alternatives to large scale thinning operations need to be developed to insure the maintenance of sufficient amounts of habitat suitable for Bicknell's Thrushes. The establishment of a mosaic of thinned and unthinned patches, or the maintenance of large islands of unthinned habitat, are two such alternatives whose merit should be assessed.

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APPENDIX. Description of vegetation composition and habitat structure variables recorded at sites occupied ($n = 42$) and unoccupied ($n = 19$) by Bicknell's Thrushes on Mont Mégantic and Mont Gosford, southern Quebec, Canada, 1997–1998.

Variable	Description
BALFIR	Importance value of balsam fir (<i>Abies balsamea</i>). Importance values were calculated as the mean of the percentage of total basal area and the percentage of total number of stems accounted for by a given taxon within a 5-m $\times$ 1-m plot.
SPRUCE	Importance value of red and white spruces (<i>Picea rubens</i> and <i>P. glauca</i>).
WBIRCH	Importance value of white birch (<i>Betula papyrifera</i>).
YBIRCH	Importance value of yellow birch (<i>Betula alleghaniensis</i>).
MTASH	Importance value of mountain ash (<i>Sorbus americana</i>).
MAPLE	Importance value of mountain maple (<i>Acer spicatum</i>).
SHRUB	Importance value of shrub species: smooth serviceberry (<i>Amelanchier laevis</i>), red-berried elder (<i>Sambucus racemosa</i>), spiny swamp currant (<i>Ribes lacustre</i>), skunk current (<i>Ribes glandulosum</i>), swamp red current (<i>Ribes triste</i>), and red raspberry (<i>Rubus idaeus</i>).
DENS5, DENS10	Vegetation density indices recorded using a 1-m $\times$ 1-m checkerboard with 20-cm $\times$ 20-cm squares held at breast height at a distance of 5 m and then 10 m from the midpoint of the 50-m transect where an observer recorded the number of partial and complete dark squares that could be seen (maximum = 13 complete squares). These measures were taken in two to four directions at 90° from one another. Vegetation density indices were calculated separately for the data at 5 m (DENS5) and 10 m (DENS10) using the following equation: $DENS = [\Sigma(26 - (2c_d + p_d))]/n$, where c_d is the number of complete squares in direction d , p_d is the number of partial squares in direction d , and n is the number of directions. A value of 26 indicates a very high density; a value of 0 indicates low density.
TOTA, TOTB, TOTC, TOTD	The number of tree stems (all species) with diameter <2.5 cm (TOTA), 2.5–5.0 cm (TOTB), 5.1–10.0 cm (TOTC), and >10.0 cm (TOTD) recorded within each 5-m $\times$ 1-m plot. Diameter was measured 20 cm above ground.
BRANA, BRANB, BRANC	The number of dead fallen trees or branches on the ground with diameter 2.5–5.0 cm (BRANA), 5.1–10.0 cm (BRANB), and >10.0 cm (BRANC), counted across the 50-m transect.
SNAG	The number of snags (standing dead trees >2 m high) recorded within each 5-m $\times$ 1-m plot.
STUMP	The number of tree stumps (<1 m high) recorded within each 5-m $\times$ 1-m plot. Stumps created both by natural means and by cutting are included in this number.
MOSS, HERB, FERN, LICH, ROCK, LITTER	Percent ground cover of MOSSes, HERBaceous plants, FERNs, LICHens, bare ROCK, and leaf LITTER estimated visually within each 5-m $\times$ 1-m plot.
USNEA	The relative abundance of <i>Usnea</i> spp. (a slow-growing lichen) within each 5-m $\times$ 1-m plot (1 = absent, 2 = present in low abundance, 3 = present in moderate abundance, 4 = present in high abundance).
CANOP, SCANOP, USHRUB, LSHRUB	The mean height in meters of the canopy (CANOP), subcanopy (SCANOP), and upper and lower shrub (USHRUB and LSHRUB) layers estimated visually within each 5-m $\times$ 1-m plot.